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Status report on development of a multispecies model of fish production¹

by

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The Northeast Fisheries Center (NEFC) research program has emphasized multi-species studies since its inception. Broad scale trawl surveys of the entire nektonic community of the region have been conducted since 1963. The benthic community of the region has also been studied during this period. The research program of the center has now evolved into a comprehensive program of ecosystem study including on-going broad scale MARMAP surveys of plankton, nekton and environmental data. The Center has collected one of the most extensive data bases on the feeding habits of adult fish that exist anywhere in the world and similar studies are now underway for larval fish. These studies are augmented by special process-oriented studies such as the experimental work on fish larvae survival conducted at our Narragansett Laboratory and the multi-ship and multi-national larval herring patch study (of the biotic and abiotic factors controlling survival) conducted in the autumn of 1979.

Our understanding of the ecosystem and the associated data base has now evolved to the stage where a multispecies model is needed to focus future laboratory and field work and efforts to formulate hypothesis on the functioning of the system. It was decided that the model should emphasize fish production because our data base is strongest here and the model results might have immediate relevance to fisheries management.

As background to the development of a multispecies model, the NEFC modeling group reviewed several models with emphasis on the Bulk-Biomass and Dynumes models by Laevastu and Favorite(1978), and the North Sea model of Anderson and Ursin (1977),

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which are the principal models designed to simulate dynamics of ecosystems with a focus on fish populations. The review of these models culminated in a two-day workshop at Harvard in December under the sponsorship of the New England Regional Fishery Management Council, Northeast Fisheries Center, and Harvard University. The general characteristics of the models were compared and their advantages and disadvantages were reviewed with respect to validity and predictive power, input data required, cost and ease of use, nature of assumptions and clarity of descriptions of biological processes, etc. The Bulk-Biomass model is a predator controlled (food unlimited) deterministic simulation procedure for estimating biomass changes within homogeneous geographic-depth strata; it does not allow for realistic recruitment functions nor recipient-donor interactions. The Dynumes model is a much more comprehensive model using time-dependent processes which allows for food-limited effects and presumably realistic (though not yet defined) recruitment functions, and interchange of energy among small subdivisions (10^0 squares) in relation to the velocity field of ocean currents and other environmental variables characteristic of the Gulf of Alaska region. Dynumes requires biomass data on all components and their interactions with biotic and abiotic factors within each square, and the data requirements are prodigious. The Anderson and Ursin(A-U) model is also a comprehensive model using differential equations to describe virtually all the basic biological and physical processes and their interactions which are known to exist in the marine ecosystem - the processes in general are realistic and clearly defined and documented but the data requirements are enormous. Both the Dynumes and A-U models are not suitable to be run in their entirety simply because much of the input data is not available (particularly prey-predator interactions) and because runs are so expensive. More important, the behavioral properties of these huge models have not yet been adequately evaluated.

There is a clear need to simplify and scale down the complexity and size of the models and at the same time utilize more empirical information on predator-prey interactions for more realistic simulation of multispecies interactions, and to use stochastic recruitment functions to describe the effects of variable recruitments. It was decided that the effects of circulation on organic production would not be emphasized in our model (like they are in Dynumes) because circulation dynamics of the New England shelf are not well known. The NEFC modeling group learned a great deal by reviewing these models. We will draw on the attributes of both models in the formulation of our own. It is important to recognize that one of the major benefits from modeling is the greater awareness of functioning of a system that results

from being forced to think about the system logically and quantitatively during the construction of the model. Thus, while it is important to learn from the review of models constructed by others, it is equally as important to learn from difficulties encountered and errors made in the construction of our own model. The NEFC model will be tailored specifically to the available data base and designed initially for efficient simulation of effects of variations in recruitment, prey-predator interactions and fishing strategies. The model will have general applicability to the entire area covered by our MARMAP program. We have called it GEORGE because the first runs will focus on Georges Bank where we have the best data.

The initial objective of GEORGE is to investigate the influence of prey-predator interactions on the fluctuations in finfish populations under various harvest strategies assuming realistic recruitment patterns. The model is intended to aid in the synthesis and analysis of the existing biological and economic data base, and to provide some guidance to the Fishery Management Councils regarding the possible long-term effects of various management strategies. In its initial form the model is not intended to simulate organic production of all the major components of the ecosystem because we do not yet have quantitative estimates of all components nor do we understand the linkages between them and the physical environment. Nevertheless we are developing GEORGE in a generalized and flexible format which can evolve and be expanded as we improve our understanding of productivity on the continental shelf.

Energy Budget for Georges Bank.

As a first step we developed a first approximation static energy budget for Georges Bank (Cohen, et al. 1978). Estimates of average annual biomass and production of phytoplankton, zooplankton, benthos, and fish were calculated and converted to $\text{Kcal/m}^2/\text{yr}$, and arrayed in the same manner as that for the North Sea after Crisp (1975). Production rates of all components appear higher than those reported for the North Sea and possible mechanisms for this higher productivity are postulated by Cohen and Wright (1978). This preliminary energy budget will be helpful in evaluating our general assumptions about partitioning energy among biological components and in placing reasonable limits on ranges of values used in simulations.

Energy Flow in the Nekton.

The next step was to examine patterns of energy flow through the nektonic community. The approach used was similar to that of Laevastu's bulk biomass model. Details of the method and the results are described

in Grosslein, Langton, and Sissenwine 1978.

The annual rate of consumption and production of six exploited species of Georges Bank was estimated for the period 1963-1972. The six species considered included both pelagics and demersals. These are the species for which the most detailed biological information is available (including population size, age composition of the population, growth rates, fecundity). They are also the species which underwent the most significant fishery induced fluctuations in abundance.

For an individual fish, consumption was related to production by an energy balance equation: $\alpha C = G+S+Q$ where C is consumption, G is growth, S is reproductive energy, Q is metabolism, and α is the assimilation coefficient. Production equals S+G. Based on the energy balance equation, annual production and consumption rates per unit area were calculated for each species, age group, and year. The production to biomass ratios for the six species ranged from 0.29 to 0.63. Consumption to biomass ratios ranged from 3.2 to 4.9. By applying these ratios to other species for which less detailed biological information was available, estimates of production and consumption were derived for the entire nektonic community during the periods 1964-1966 and 1973-1975. The first period represents an era of developing foreign exploitation of the Georges Bank region. The second period follows nearly a decade of intense exploitation. The results are summarized in Table 1.

Both consumption and average biomass declined by about 42% from 1964-1966 to 1973-1975, but production declined only by 26%. The smaller reduction in production primarily reflects a decline in herring which have a low production to biomass ratio and an increase in the abundance of squid which are assumed to have a high production to biomass ratio. Both pelagic and demersal species declined in abundance. It is noteworthy, that during both periods, consumption by silver hake exceeds total production of the nektonic community. Extensive analysis of the gut contents of silver hake indicate that the species primarily feeds on other fish. This implies that silver hake must be feeding heavily on prerecruit fish (fish less than one year of age were not included in this analysis) which could make recruitment to finfish stocks strongly dependent on silver hake biomass.

Feeding Interactions

Various feeding functions are being investigated. For example, we may suppose that a fish feeds until it fulfills its daily feeding requirement. The size of this meal has been described as a power function of the predator's weight (Ration = aw^b , where w = weight, Andersen and Ursin, 1977) and an exponential function of temperature (Ration = $R_{\max} [\exp(Q_{10} * \text{temp})]$ Kremer and Nixon, 1978). Whether or not the predator consumes this entire meal depends on the availability of prey. The fraction of this meal that is actually consumed can be described for example by an Ivlev (1961) type function (FRAC = $1 - e^{-kp}$). The species composition of this meal is complicated in a multispecies model. Feeding functions which take into account food preference (both size and food type) and digestion rates for various prey are being developed, based on the literature on feeding and digestion of fish and on extensive analysis of fish stomach contents by NEFC (Grosslein, et al. 1978; Edwards and Bowman 1978; Bowman, et al. 1976). Rich Langton and Ed Cohen will be working cooperatively with Jan Beyer in exploring the application of queuing theory in the simulation of feeding behavior, digestion, and estimation of daily rations.

Stochastic Simulation of Recruitment.

Recruitment is the dominant process determining biological productivity of Georges Bank fish stocks. Therefore, the recruitment process must be carefully considered in the development of an ecosystem simulation model of the region. Unfortunately, a clear understanding of the factors that control recruitment is lacking for Georges Bank and virtually all other ecosystems. Thus, in order to introduce a degree of realism into an evolving ecosystem simulation of Georges Bank, it has been decided that recruitment will be simulated stochastically.

An analysis of the available data describing recruitment for the Georges Bank finfish and squid community has been undertaken. Estimates of the strength of recruiting year classes and the size of their parent spawning stock have been collected for the following species: cod, haddock, silver hake, yellowtail flounder, pollock, red hake, long-finned squid, short-finned squid, herring, and mackerel. In most cases, about 10 observations of recruitment are included, but for some species as many as 30 observations are available. The frequency distribution of recruitment for each species has been compared to both a normal and a lognormal

distribution. Only for haddock is the frequency distribution of recruitment significantly different from either the normal or lognormal distributions. Of course, because of the small number of observations available, the power of statistical "goodness of fit" tests was low.

The time series of recruitment observations for each species was also tested for independence (of sequential observations). Recruitment was positively autocorrelated for half of the species considered.

The relationship between spawning stock size and recruitment is now being investigated. Past experience indicates that a statistically significant relationship between these variables is unlikely for most species. In any case, subroutines are being written that will simulate recruitment stochastically based on distribution of past observations. These Monte Carlo simulations may be based on conditional probability density functions which incorporate the effects of sequential dependence between observations (autocorrelation), spawning stock size and or other factors. The subroutines will be incorporated into the Georges Bank ecosystem simulation model.

Thus, at this time, it is anticipated that recruitment of each species will be simulated without a detailed representation of its early life history. Nevertheless, prerecruit compartments will be included in the model in order to maintain accountability for all energy transfers. Energy will be transferred from the adult fish compartments of the model to the prerecruit compartment at the time of spawning. The growth rate of prerecruit fish and their pattern of mortality (a vector of relative mortality rates for each stage of the prerecruit phase) will be entered into the model exogenously as parameters. The mortality pattern will be adjusted by a variable multiplier so that the resultant frequency distribution of recruitment will correspond to the output of the stochastic recruitment simulation subroutine described above. The energy necessary to support growth of individuals of the prerecruit compartment will be transferred from likely prey compartments (primarily secondary carnivores). The energy flow from the prerecruit compartment as a result of mortality will be directed to predatory fish compartments (based on their feeding rate as determined by feeding functions), the detritus compartment and benthos compartments.

In future refined versions of the model, more detailed representation

of prerecruit processes (including species interactions and negative feedback between prerecruit and recruit compartments) may be possible. Our understanding of the early life history of marine fish and the data base describing the corresponding processes is at present inadequate for the more refined simulation model.

General Description of the Model.

The general form of the model GEORGE is $\frac{dx}{dt} = A \underline{x} + \underline{f} + \underline{b}$, where \underline{x} is the species biomass vector. This \underline{x} vector includes the juvenile and adult classes of both predator and prey species. The community matrix, A , describes the transfers between predator-prey compartments (R. May, 1973). The \underline{f} and \underline{b} vectors represent the fish lost to fishermen, and the fish recruited to the population per time step dt , respectively. In GEORGE I, the linear version, A , \underline{f} , and \underline{b} are constant coefficients. In GEORGE II, the deterministic nonlinear version, A , \underline{f} , and \underline{b} are functions of the biomass vector and environmental signals such as time and temperature. In the stochastic, nonlinear models GEORGE III, a degree of random variability is placed around the estimates of A , \underline{f} , and \underline{b} . In all three models, provisions are made for variable time steps. In the later two versions, the A and \underline{f} and \underline{b} are re-estimated between each time step.

In the linear version, GEORGE I, the behavior of the model is determined solely by the A , \underline{f} and \underline{b} vectors. In the nonlinear versions, the behavior is determined by interaction of six subroutines (UPDATE, CATCH, FEED, DEMAND, GROW, COEFS) which operate in sequence to control the processes of recruitment, growth, and mortality. Various parts of these processes have been put in separate compartments (the six subroutines) to simplify program changes and to aid in the interpretation of simulation results. The six subroutines are themselves controlled by a seventh subroutine called INTERACT. For each time step INTERACT serves like a directory, sequentially calling on the other six subroutines.

The first subroutine, UPDATE, computes natural changes in the biomass vector, \underline{x} , that are the result of recruitment, natural mortality, and migration. The biomass vector includes age as well as species composition (i.e. the first n_1 -elements of \underline{x} , represent the n -age classes of species-1, while the second n_2 -elements represent the n_2 -age classes of species-2, etc.). With every time step, UPDATE corrects \underline{x} for changes due to natural mortality or migration into or out of the study area. UPDATE also "ages"

the fish stocks, incrementing their passage from one age class to the next at appropriate times. The recruitment process (entry of age 1 individuals) in UPDATE will be simulated by a function based on the observed data. In short, UPDATE determines the current state of the vector x based on its state in the previous time interval and the rates of processes responsible for change during the current time step.

The second subroutine, CATCH, determines the amount of fish harvested per time step. This harvest will depend on the fishing strategies (e.g. species quotas) set by the user which take into account the availability of fish, by-catches, economic yield per unit effort, etc.

The next three subroutines, FEED, DEMAND, and GROW deal with growth. The changes in fish biomass are calculated as the difference between inputs and losses. For inputs, subroutine FEED computes prey consumption taking into account prey-predator interactions and fluctuations in abundance of prey as well as predators. Various feeding functions will be investigated as described above.

Given these inputs, the subroutine DEMAND computes the losses from the fish. This involves assimilation efficiencies and the basal and active respiratory losses. Assimilation is a function of gut efficiency and represents the fraction of the ingested material that is not defecated. Basal respiration is a physiological maintenance cost, and is a function of age and the temperature. Active respiration represents the losses incurred during swimming, feeding, and breeding activities.

The growth realized is the difference between the uptake simulated in FEED, and the digestive and respiratory losses computed in DEMAND - and is calculated in subroutine GROW. This surplus of material is then partitioned between somatic and reproductive tissue, and represents growth (There is always the possibility that negative growth, i.e. weight loss, may occur when energy requirements exceed inputs).

The sixth and last subroutine, COEFS recomputes the community matrix, A , (R. Levins, 1968) and stores it along with the f and b vectors for computation in the next time step. This community matrix is the result of the processes computed in the five previous subroutines. The utility of this subroutine will be discussed in a following section on sensitivity analysis.

Modeling options.

To run the model, the user first specifies the run parameters and program coding changes through the input/interactive portion of the program. The user then specifies the numbers of years to be simulated, as well as the desired time step within each year. To examine the results of the simulation the user can specify which populations should be included in the output tables. After glancing at these tables, the user then has the option of generating plots of populations of interest.

After examining the tables and graphs, the user has the option of stopping or continuing. Should the user decide to continue, there are the options, RESUME and BACKUP. RESUME allows the user to continue the simulation with or without changing the model's hypotheses in the interim. BACKUP allows the user to resimulate a portion of the previous run, under different hypotheses. This BACKUP option allows the user to test a series of policy scenarios, without having to resimulate the years prior to the target date.

Sensitivity Analysis of Models.

In single species models, stability and system behavior can be probed by the selective "tweaking" of coefficients. However, the relationship between input changes and output becomes increasingly clouded, with the increasing complexity of the model. This is especially difficult to assess at the multispecies level of complexity.

In the nonlinear models (using GEORGE II and GEORGE III) the user has the additional option of analyzing A, the community matrix and the f and b fishing and recruitment vectors. These components serve as "snapshots" of the dynamics of the system during a given timestep. The stability of the system and the trends of the predators and prey within the system can be studied in detail by inputting A, f and b into the linear model GEORGE I. This serves to expand and exaggerate the changes occurring in the nonlinear model, giving the user a feel of the ultimate direction of changes to be expected in the nonlinear runs.

As the coefficients are constant within a timestep and can be assumed (pretended) to be slowly changing, the traditional linear analysis methods can be applied. This would include the examination of the community matrix's eigenvalues (J. Poole, 1974). The stability and behavior of the

system can be inferred from the real or imaginary eigenvalues, and the sign of these eigenvalues (Takahashi, Rabins, Auslander, 1972; E. Bender, 1978; H. Gold, 1977).

A Time Table.

The linear version, GEORGE I, was completed in August 1978, and we hope to have the deterministic, nonlinear version, GEORGE II running in 1979. From the biological standpoint the most troublesome aspect probably will be the formulation of feeding functions and prey-predator interactions, particularly those affecting juvenile stages of fishes. For the time being we will not attempt to deal with causality in the recruitment function, but simply use available time series as a statistical basis for generating realistic variability in recruitment up to the juvenile stage (age 1). Factors affecting fishing strategy will be handled by the Assessment Group. Other groups (New England Council staff, and Wm. Bossert, Harvard) are also involved in development of such models, and the council staff plans to complete their prototype model by early 1979, which will attempt to construct a stock rebuilding strategy such that the gross revenues are maximized.

In another year or so, it is anticipated that we will have sufficient new information on primary and secondary production (and also apex predators and birds) such that it will be possible to refine our energy budget calculations for the shelf. In addition, a benthic nutrient regenerative system model for the shelf is being developed by Wendell Hahn, a graduate student at URI Graduate School of Oceanography. Thus by mid-1980 we may be able to add the rest of the basic biological components to GEORGE, at least to a first approximation. It is still too early to predict how soon we may be able to link up organic production and shelf circulation in a quantitative way.

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Table 1. GEORGES BANK CONSUMPTION AND PRODUCTION IN THOUSANDS OF KILOCALORIES PER KILOMETER SQUARED.

Species Group	1964-1966			1973-1975		
	Biomass	Consumption	Production	Biomass	Consumption	Production
Cod	1890	5561	1071	920	3036	552
Haddock	4474	16117	2147	443	1418	182
Redfish	23	69	6	53	159	13
Silver hake	10052	48587	5830	7412	36318	4373
Red hake	1084	4444	499	801	3284	368
Pollock	278	1140	128	118	484	54
Yellowtail flounder	626	2874	399	481	2213	303
Other flounder	312	1279	144	239	980	110
Herring	19261	87521	5393	6201	28525	1798
Mackerel	1314	5410	446	2730	11739	928
Other finfish	1684	6904	775	2260	9266	1040
Illex	231	1617	247	1719	12033	2579
Loligo	63	441	95	273	1911	410
Total	41292	192064	17160	23650	111366	12710